SEX-DETERMINATION AND BIOLOGY OF A PARASITIC WASP, HADROBRACON BREVICORNIS (WESMAEL).

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The problem of sex-determination is nowhere of greater interest than in the Hymenoptera. The occurrence of parthenogenesis as well as sexual reproduction adds interest to this matter, especially in view of the fact that considerable variation in conditions obtains, not only between the different families, but even between the minor groups of the same family.

The present studies deal with an insect, *Hadrobracon brevicornis* (Wesmael), belonging to the family Braconidæ.

The insects vary greatly in coloration, ranging from near black though various intermediate patterns to near yellow. In the near-yellow individuals black pigment usually persists in the antennæ, in the compound eyes, about the ocelli, and in small markings near the base of the wings. No experiments have been made to test the cause of color variation except that it has been shown that it does not yield to selection. It seems probable, therefore, that it is due to some environmental influence. It shows a certain correlation with size, for the dwarfed specimens are usually very dark while the larger individuals are either very light or of intermediate color. There is no apparent correlation of color with sex.

In view of the fact that genetic differences with respect to color exist in the honey-bee, I had expected the yellow and the black variations of *Hadrobracon* to reproduce themselves, but this is not the case.

Fig. 1, *A*, shows a light colored male and Fig. 1, *B*, shows a rather dark female. Sexual dimorphism is evident in the longer antennæ of the male and in the presence of the ovipositor of the female. Variation occurs in the number of antennal joints and in the general body size. The larger specimens are three to four

millimeters in length, but minute individuals occur as well. The latter are probably starved. They are fertile, nevertheless, and give rise, when bred, to wasps of normal size.

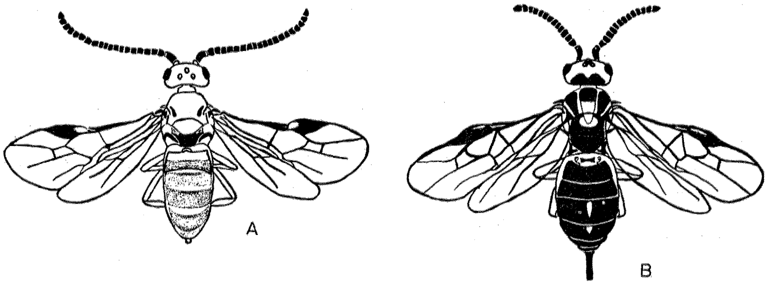

FIG. 1.

The insects mate readily as soon as they emerge from their white silken cocoons. The females deposit their eggs upon the bodies of full-grown caterpillars of the Mediterranean flour-moth, *Ephestia kuehniella* Zeller, and probably also upon other meal caterpillars. The caterpillars are stupefied by the sting of the wasps and remain quiet until the acephalous, apodous larvæ emerge and devour them. Several eggs are laid upon one caterpillar and as many as ten or a dozen wasps will sometimes develop. Usually the number is smaller. At a high temperature the length of a generation is ten days or less. The adult females may live as long as six weeks.

The work has been handicapped by lack of sufficient caterpillars at necessary times. As a consequence I have not been able to rear as many offspring as desired. The greatest number of progeny obtained from a single female was one hundred and twenty-eight, but I am convinced that many more could be secured if sufficient food were available. The technique of rearing and handling the moths is being developed and it is hoped that further work upon the wasps may be done as a result.

A protozoan parasite has been found in the caterpillars and in *Hadrobracon*. It has been eliminated by heat sterilization of the food and glassware. Its life history is being worked out by Dr. D. H. Wenrich. The small numbers in some of the families of *Hadrobracon* are due to the presence of this parasite.

My thanks are due to Dr. McClung for the facilities of the

Table I.

Inbred Progenies of Mated Females.

Designation of Parents.	Offspring.		
	Generation.	Sex.	
		♂.	♀.
♀ no. 1	F_1	49	47
F_1a	F_2	34	56
F_1b	F_2	26	29
F_1c	F_2	31	48
F_1d	F_2	31	47
Total..................	F_2	122	180
F_2a from F_1a	F_3	6	17
F_2b " F_1a	F_3	3	9
F_2c " F_1a	F_3	8	10
F_2t " F_1a	F_3	2	10
Total..................	F_3 from F_1a	19	46
F_2d from F_1b	F_3	10	9
F_2q " F_1b	F_3	2	8
F_2p " F_1b	F_3	11	8
F_2o " F_1b	F_3	21	13
F_2n " F_1b	F_3	5	13
F_2k " F_1b	F_3	15	18
Total..................	F_3 from F_1b	64	69
F_2e from F_1c	F_3	4	12
F_21 " F_1c	F_3	25	18
Total..................	F_3 from F_1c	29	30
F_2i from F_1d	F_3	2	6
F_2j " F_1d	F_3	1	5
F_2m " F_1d	F_3	13	13
Total..................	F_3 from F_1d	16	24
Total..................	F_3	128	179
F_31 from F_2a	F_4	5	23
F_32 " F_2a	F_4	17	18
F_33 " F_2a	F_4	18	19
F_34 " F_2a	F_4	11	27
Total..................	F_4 from F_2a	51	87
F_36 from F_2q	F_4	15	28
F_37 " F_2q	F_4	11	31
F_38 " F_2q	F_4	10	23
F_310 " F_2q	F_4	7	10
Total..................	F_4 from F_2q	43	92
F_3 12 ♀ from F_2t	F_4	21	39
Total..................	F_4	115	218

TABLE I.—*Continued.*

Designation of Parents.	Offspring.		
	Generation.	Sex.	
		♂.	♀.
F_4a	F_5	4	6
F_4b	F_5	8	22
F_4c	F_5	9	12
F_4g	F_5	4	3
F_4p ♀ from $F_3$6	F_5	19	19
F_4w ♀ " $F_3$6	F_5	12	12
F_4y ♀ " $F_3$8	F_5	26	25
$F_4$14	F_5	32	48
$F_4$15	F_5	7	19
Total..................	F_5	121	166
F_5a	F_6	14	9
F_5g	F_6	2	9
F_5m	F_6	5	6
Total..................	F_6	21	24
F_6g2	F_7	2	3
F_6g3	F_7	8	7
F_6k	F_7	2	4
F_6h	F_7	1	1
Total..................	F_7	13	15
F_7b	F_8	1	1
F_7c	F_8	8	9
F_7d	F_8	2	3
F_7e	F_8	0	1
Total..................	F_8	11	14
F_8a	F_9	4	2
F_8d	F_9	9	1
Total..................	F_9	13	3
	Total from 51 mated females	593 ♂♂	846 ♀♀

laboratory and for his kindly help and criticism. The work has been done by aid of a Harrison Research Fellowship of the University of Pennsylvania.

In November, 1916, a female wasp (♀ No. 1) was found in cultures of the Mediterranean flour-moth at the Zoölogical Laboratory. A little later some cocoons of the wasp were found and these were isolated in vials. Both males and females emerged from the cocoons. The females were not mated but produced parthenogenetically families consisting entirely of males.

The first female (♀ No. 1), produced forty-nine males and forty-seven females. As later results show she had in all probability mated. Table I. shows the progeny of mated females descended from ♀ No. 1. No variation of sex-ratio correlated with age of the mother or lapse of time since mating could be detected.

The first column of Table I. gives the designation of the parents. The various matings of a given generation are designated by the letters of the alphabet, as F_3a, F_3b, etc. In case there are more than twenty-six matings in any generation, the succeeding matings are numbered, as F_31, F_32, etc.

Omission of letters or numbers denotes that the parents in question are elsewhere summarized or else produced no offspring.

The second column denotes the generation of the offspring and the third and fourth columns denote the males and females respectively.

The points of interest to be noted in Table I. are as follows:

Each of the fifty-one females produced females, and all but F_7e, which produced a single female only, produced males.

Considerable variation in sex ratio obtains in different fraternities, usually with excess or equality of females.

An attempt to correlate sex ratio in the maternal fraternities with that of the progeny resulted as follows:

Matings of progeny of	F_1a	(34 ♂♂ : 56 ♀♀)	gave	(19 ♂♂ : 46 ♀♀)
"	F_1c	(31 ♂♂ : 48 ♀♀)	"	(29 ♂♂ : 30 ♀♀)
"	F_1d	(31 ♂♂ : 47 ♀♀)	"	(16 ♂♂ : 24 ♀♀)
"	F_2a	(6 ♂♂ : 17 ♀♀)	"	(51 ♂♂ : 87 ♀♀)
"	F_2q	(2 ♂♂ : 8 ♀♀)	"	(43 ♂♂ : 92 ♀♀)
"	F_2t	(2 ♂♂ : 10 ♀♀)	"	(21 ♂♂ : 39 ♀♀)
"	F_36	(15 ♂♂ : 28 ♀♀)	"	(31 ♂♂ : 31 ♀♀)
"	F_38	(10 ♂♂ : 23 ♀♀)	"	(26 ♂♂ : 25 ♀♀)

Fraternities with excess females (131 ♂♂ : 237 ♀♀) gave 236 ♂♂ : 374 ♀♀ = 1 : 1.6.

Matings of progeny of	♀ no. 1	(49 ♂♂ : 47 ♀♀)	gave	122 ♂♂ : 180 ♀♀
"	F_1b	(26 ♂♂ : 29 ♀♀)	"	64 ♂♂ : 69 ♀♀

Fraternities with equality of sexes (75 ♂♂ : 76 ♀♀) gave 186 ♂♂ : 249 ♀♀ = 1 : 1.3.

It is seen that a higher female ratio is obtained in the progeny of those fraternities in which the females were in excess of the

males than in the progeny of those fraternities in which the sexes were equal, but although this condition obtains the numbers are too small and the exceptions too numerous to be conclusive. Thus the progeny of F_1c, $F_3$6 and $F_3$8 had excess of females but produced equality of sexes, while the progeny of ♀ No. 1 had equality of sexes but produced excess of females.

As mentioned earlier in the paper, virgin females gave only male offspring.

Twenty-six virgin females were isolated and produced 757 males. The fraternities consisted of 4 to 84 individuals. Eight females that were with males produced 146 males and no females. It is probable that they did not mate.

TABLE II.

OFFSPRING OF FEMALES, BEFORE AND AFTER MATING.

Designation of Parents.	Offspring.		
	Before Mating, ♂♂.	After Mating.	
		♂♂.	♀♀.
		to other than their own sons	
v ♀ 2	106	13	9
$F_3$11	7	5	2
F_5c	20	1	6
		to their own sons	
F_3f	7	5	7
F_4i	59	51	0
F_4n	16	11	27
F_4o	50	11	11
F_4l	30	0	2
F_5j	41	42	6
F_6a	40	2	2
Total from ten ♀ ♀	376 ♂♂	90 ♂♂ (excluding F_4i)	72 ♀♀

Total from thirty-six virgin females—1,133 ♂♂.

Total from sixty-one mated females (excluding those that were set with males but produced only males)—683 ♂♂, 918 ♀♀.

Table II. shows the progeny of ten females that were mated late in life after they had produced several males. Seven of these were mated to their own parthenogenetically produced sons. In every case only males were produced before the mother mated and nine of the mothers produced daughters after mating. Virgin female F_4i produced fifty-one males after being introduced to a male. It is probable then that she did not mate.

The excess of males (90 : 72) in the progeny of females mated late in life is probably due to the fact that they did not mate after being set with a male until after they had laid a few eggs.

Summarizing then we have sixty-one females set with males that produced both males and females (683 : 918), nine that produced only males (197) and thirty-six virgin females that produced only males (1133). *Not a single female has been produced from a virgin female.*

The conclusion might be drawn then that in *Hadrobracon brevicornis* fertilized eggs produce females and unfertilized eggs produce males. If this is comparable with conditions in the honey-bee and the hornet, it must be supposed that the male is a haplont; the female, a diplont. An alternative possibility would be that males are diplonts, in which case they might be formed either from unreduced eggs or from reduced eggs that have been fertilized by male-determining spermatozoa.

Cytological work is now in progress that confirms the theory that the male is haplont. The first spermatocyte division is abortive as in the honey-bee. Details will be published later.

Other work in regard to sex-determination in the Braconidæ is that of F. M. Webster (1909) and S. J. Hunter (1909) on *Lysiphlebus tritici*, belonging to the subfamily Aphidiinæ. The results of these investigations have been reviewed and discussed by A. F. Shull (1910). Both males and females were produced from mated females. Virgin females usually produced males but occasionally a few females.

The work done at the United States Parasite Laboratory at Melrose Highlands, Mass., indicates that males are usually produced from virgin females of Braconids and Ichneumonids, but Hemiteles, an Ichneumonid hyperparasite, produces females parthenogenetically as well.

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